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DESCRIPTION, OSTEOLOGY AND RELATIONSHIPS OF
THE AMAZONIAN CYPRINODONT FISH *FLUVIPHYLAX*
PYGMAEUS (MYERS AND CARVALHO)Tyson R. Roberts¹

ABSTRACT. The minute Amazonian cyprinodontid *Fluviphylax pygmaeus* (Myers and Carvalho) is redescribed and its osteology worked out based on material obtained by the Expedição Permanente da Amazônia (EPA). Its relationships apparently lie either with the Procatopodinae (a subfamily otherwise restricted to Africa) or with the Fundulinae, and not with the Rivulinae. A new subfamily, Fluviphylacinae, is proposed for it. The very smallest egg-laying and live-bearing cyprinodonts occur in Amazônia, whereas the largest ones are found in habitats geographically or ecologically isolated from rich fish faunas.

ACKNOWLEDGEMENTS

I wish to thank Prof. George S. Myers, Division of Systematic Biology, Stanford University, and Dr. Neal R. Foster, Department of Limnology, Academy of Natural Sciences of Philadelphia, for critically reviewing the manuscript of this paper and offering helpful suggestions.

INTRODUCTION

This paper deals with an almost unknown but widely distributed Amazonian cyprinodontid fish of minute size, *Fluviphylax pygmaeus* (Myers and Carvalho). Prof. George S. Myers of Stanford University kindly supplied the following information about its original discovery. In 1942-44, when Myers was working at the Museu Nacional in Rio de Janeiro in collaboration with Sr. Antenor Leitão de Carvalho, Naturalista of the Museu, a man named Alexandre Parko was collecting for the Museu in Amazonia. Although primarily concerned with insects, Parko obtained a few vertebrates, including the type of a remarkable toad, *Bufo dapsilus* Myers and

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Carvalho (1945a), from Benjamin Constant, and the type of a strange, leaf-nosed lizard, *Anolis phyllorhinus* Myers and Carvalho (1945b), from Borba on the lower Rio Madeira.

The Parko material from Borba also included specimens of a remarkable new genus and species of minute cyprinodontid with enormous eyes, obviously closely related neither to *Rivulus* nor to any other previously described South American member of the family. Myers already had been aware that a cyprinodontid of this type existed in Amazonas; as a student under the late Prof. Carl H. Eigenmann he had found one partially squashed and otherwise poorly preserved specimen from the lower Rio Amazonas while unpacking fishes collected by the late Carl Ternetz in 1923-25. This specimen was in no condition for description and seems eventually to have become lost. Carvalho and Myers planned to describe the Parko specimens, but Myers had to leave Rio before this was done, bringing with him to Stanford only three specimens. Later, when Carvalho was at Stanford on a Guggenheim Fellowship, some more work was done on the fish, and Carvalho prepared a drawing of it. Unfortunately the drawing and data were lost in the late 1950's.

While preparing a resumé of cyprinodontid subfamilies, Myers (1955) gave a brief diagnosis of Parko's tiny Amazonian fish, which now may be reproduced:

One new fish that aquarists will probably see before too long is the very tiny *Potamophylax pygmaeus* Myers and Carvalho, from the Middle Amazon. It is one of the smallest of all killies, and its place in the above classification is not clear. The strange characteristics, as worked out by Mr. Carvalho and me, include enormous eyes, a dorsal fin set entirely behind the anal fin, high-set pectoral fins and a deep "pocket" beside the latter fin. It represents a hitherto unknown genus and species and it may be related to the African lampeyes.

Although no type specimens were designated, the description satisfied the rules of zoological nomenclature in effect at the time it was published, and therefore is nomenclaturally valid. Whitley (1965: 25) pointed out that *Potamophylax* Myers and Carvalho is preoccupied by *Potamophylax* Wallengren, 1891 (a neuropteran insect), and proposed the substitute name *Fluviphylax*, with *P. pygmaeus* as type species. The species apparently never has been imported as an aquarium fish and nothing further has been reported about it.

Since the types are few in number and only in fair condition, it

was highly desirable to obtain more material. In 1968 I participated in field work in Amazonas as a member of the Expedição Permanente da Amazônia. EPA is a continuing, cooperative effort among the Museu Goeldi in Belem, the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, and the Museu de Zoologia of the Universidade de São Paulo (MZUSP),¹ financed by the Fundação de Amparo à Pesquisa of the state of São Paulo. I wish to thank Dr. P. E. Vanzolini, Director of the Museu de Zoologia, for arranging my participation. September 20 through November 5 we worked on the Rio Solimões between Manaus and Santo Antonio do Içá (the Middle Amazon). The scientific party consisted of Heraldo A. Britski (leader), Júlio Cesar de Garavello, Silvia Gerken, Naercio A. Menezes and myself. Our primary purpose was to collect fishes and we were fortunate in obtaining *Fluviphylax* at several localities. The extensive collections from this trip are being sorted at the Museu de Zoologia. Additional *Fluviphylax* were located in the material obtained by EPA on the Lower Amazon in 1967 (its first year in operation). With the kind permission of Heraldo Britski, who is in charge of the fish collections, I brought two lots to the United States for this study. Finally, it is of considerable interest to note that the Museum of Comparative Zoology has a few small lots of *Fluviphylax* obtained by the Thayer Expedition under Louis Agassiz in 1866. In all probability Garman had the Agassiz specimens in hand when he wrote his monograph, "The Cyprinodonts" (Garman, 1895), but passed them over as the young of *Rivulus*.

Since they are liable to be confused, care has been taken to distinguish *Rivulus* from *Fluviphylax* in the following generic characterization. The easiest distinctions to use involve eye size, nature of orbital rim, number of suborbital scale rows, width of head, condition of anterior nostril, jaw structure, and relative positions of pectoral and pelvic fins.

Genus FLUVIPHYLAX Whitley

Potamophylax Myers and Carvalho, in Myers, 1955: 7 (original description: type species *P. pygmaeus* Myers and Carvalho, by original designation: name preoccupied by *Potamophylax* Wallengren, 1891, a neuropteran insect).

¹ Formerly Departamento de Zoologia of the Secretaria da Agricultura of the state of São Paulo. The name was changed in June, 1969, when it became part of the Universidade de São Paulo.

Fluviphylax Whitley, 1965: 25 (replacement name for *Potamophylax* Myers and Carvalho, and therefore taking same monotype).

Characteristics. Tiny egg-laying cyprinodonts, widespread in Amazonas, typically found in still backwaters. Largest specimen available for measurement 18.5 mm; females as small as 14.5 mm with ripe ovaries.¹ Body moderately elongate, sub-cylindrical in cross-section, sides not compressed. Body axis straight. Head about as wide as deep (head considerably wider than deep in *Rivulus*). Eye extremely large, nearly as deep as head, its dorsal margin either flush with dorsal contour of head or barely below it, and largely exposed dorsally (supraorbital portion of frontal bone only partially covering eye); orbital rim free (eye of moderate size, covered dorsally, and with attached orbital rim in *Rivulus*). Pre-orbital space narrow, about .25 diameter of eye. Interspace between eye and upper angle of preopercle extremely narrow; preopercular segment of cephalic sensory canal system very close to posterior margin of eye. A single row of scales extending just below eye. Below this suborbital scale row the interopercle can be lifted sideways to reveal a deep furrow in the skin separating geniohyoideus muscles from jaw suspension (there are at least two or three suborbital scale rows in *Rivulus*, and the area between geniohyoideus muscles and jaw suspension is smooth and scaled over). Snout short, about .5 eye diameter, its dorsal contour with a slight concavity anterior to eye. Anterior nasal opening a pore flush with snout (tubular in *Rivulus*). All segments of cephalic sensory canal usually open, but a few specimens have one or more of the segments closed. Some scales of midlateral series with pit organs. Mouth small, superior, the small upturned jaws set at an angle of about 45 degrees (mouth less superior in *Rivulus*, with a very characteristic, deep, right-angled notch or recess between nasal and lacrimal bones into which rictal membranes fit). Jaw teeth conical, in two irregular rows in both jaws, teeth of outer and inner rows of about the same size. Tongue free from floor of mouth for most of its length; rounded in cross-section near the tip, posteriorly a somewhat flattened triangle in cross-section (with apex downward and lying between left and right m. geniohyoidei) (in *Rivulus* tongue attached to floor of mouth except for its anterior third, flattened in cross-section throughout its free portion, and broadly rounded or blunt at tip). No teeth on palate (prevomer usually bearing teeth in *Rivulus*). Intestine in anterior third of body forming one and a

¹ Standard lengths only are recorded in this paper.

half vertical loops at an angle of about 30 degrees to body axis (anterior portion of looping to left and posterior portion to right side of body); straight in remaining two-thirds of body cavity. Stomachs of numerous specimens contain minute insect larvae. Gill rakers smooth, slender shafts, widely set, ten on lower and two or three on upper limb of first gill arch. Pseudobranch an ovoid, bilobate, white, glandlike mass without filaments about .5 mm high in a 16-mm specimen, covered by a transparent membrane. Origin of gill opening about .25 eye diameter in front of pectoral fin base, on a level with or slightly below origin of uppermost pectoral ray. Gill membranes free from isthmus, united to each other at a point on a vertical with posterior margin of eye. Branchiostegal rays usually five on either side.

Dorsal fin small, with five or six rays, its origin distinctly posterior to a vertical line through base of last anal ray (dorsal fin set equally far back in some species of *Rivulus*, but usually with more rays). Anal fin much larger than dorsal, with eight or nine rays. Anal fin pterygiophores slender except for the first, which is moderately expanded. Caudal fin rounded. Pectoral fins high-set, uppermost pectoral ray originating distinctly above lateral midline of body, and extending well beyond base of pelvic fin (uppermost pectoral ray inserted below midline in *Rivulus*, and pectoral fin failing to reach pelvic base). Internal to base of pectoral fin a deep pocket, the entrance to which is guarded by delicate tissues easily ruptured (similar pockets present in all cyprinodonts). Pelvic fins separate, not connected by membrane, with six rays. Pelvic insertion equidistant between origin of lowermost pectoral ray and anal fin origin.

In mature males dorsal, pelvic, and anal rays slightly to moderately elongated, and dorsal, pelvic, anal and caudal fins with a barred pattern (strongest on anal and caudal). Shape of caudal fin unaffected by sexual dimorphism. Examination of scales and fins with direct and transmitted light failed to reveal contact organs. Ripe females contain 30-40 eggs, the largest of which are somewhat over .1 mm in diameter, and their abdomens are slightly distended (best seen viewing specimen from above). Teasing the surface of eggs isolated from the ovary reveals elongate chorionic filaments which apparently originate from a restricted portion of the chorion, but no short, spinelike projections (short, spinelike projections are distributed over the entire chorionic surface in various atherinoids, *Oryzias* and *Horaichthys*). Ovary single, without indication of division between right and left halves. Males with cloacal-genital area unswollen, a small, distinctly tubular opening

to sperm duct slightly in advance of base of first anal ray. Some females with cloacal-genital area considerably swollen, an oviducal pouch opening in front of first anal ray (the membranes of this pouch do not encroach upon first anal ray, nor do they extend along side of anal fin base, as happens in some Fundulinae).

Fluviphylax pygmaeus (Myers and Carvalho)

Figures 1 and 2

Potamophylax pygmaeus Myers and Carvalho, in Myers, 1955: 7 (original description; type locality "Middle Amazon"—Borba, lower Rio Madeira; types in Museu Nacional, Rio de Janeiro; three paratypes at Stanford).

Fluviphylax pygmaeus Whitley, 1965: 25 (name only).

Material studied. SU 50196, three paratypes 14.9-16.1 mm, Rio Madeira at Borba, collected in 1943 by A. Parko; MZUSP 6245, 13 specimens 11.5-18.5 mm, "lago above Manaus," margem esquerda Rio Negro, Amazonas, Brasil, collected by EPA April 28, 1967; MZUSP 5590, 50 specimens 9.9-17.0 mm, Lago Parauacui, near Oriximina, Pará, Brasil, February 9, 1967, EPA; MCZ 41367, five specimens 12.9-14.4 mm, Lago Hyanuary, Amazonas, Brasil, 1865-66, Thayer Expedition; MCZ 6262, five specimens 10.3-10.5 mm, Obidos, Pará, Brasil, 1865-66, Thayer Expedition; MCZ 6265, one specimen 12.9 mm Lago Alexo,¹ Amazonas, Brasil, 1865-66, Thayer Expedition.

¹ In response to my inquiry, Prof. Myers provided the following information about this locality:

Many Thayer Expedition fishes came from Lago Alexo. The name may be misspelt, as are some other Thayer localities. It may have been "Lagôa Aleixo." However, there is no such place listed, spelt either way, in the 4 volumes of Pinto's "Diccionario Geographico," including the several little addenda at the ends of the volumes. "Journey in Brazil," the narrative of the Thayer Expedition by Louis and Mrs. Agassiz, has no index and does not give a complete itinerary of the separate trips made by expedition members in the Amazon. However, on p. 294, it records the return of Thayer to Manaus on December 6, 1865. Going backward in the book, the last previous mention of Thayer is on p. 282, where it says that he and Bourget were sent (from Manaus) to "Lake Cudajas, to be gone ten days," this being recorded under the date of November 20. That is, unless two separate small trips were involved, which is doubtful, Thayer started for "Lake Cudajas" on November 20 and "returned from Lago Alexo" 16 days later. "Lago Alexo" may be the same as "Lake Cudajas," the correct name of which Thayer could have found to be "Lago Alexo" once he got there. In any event, Lago Alexo cannot be far from Manaus.

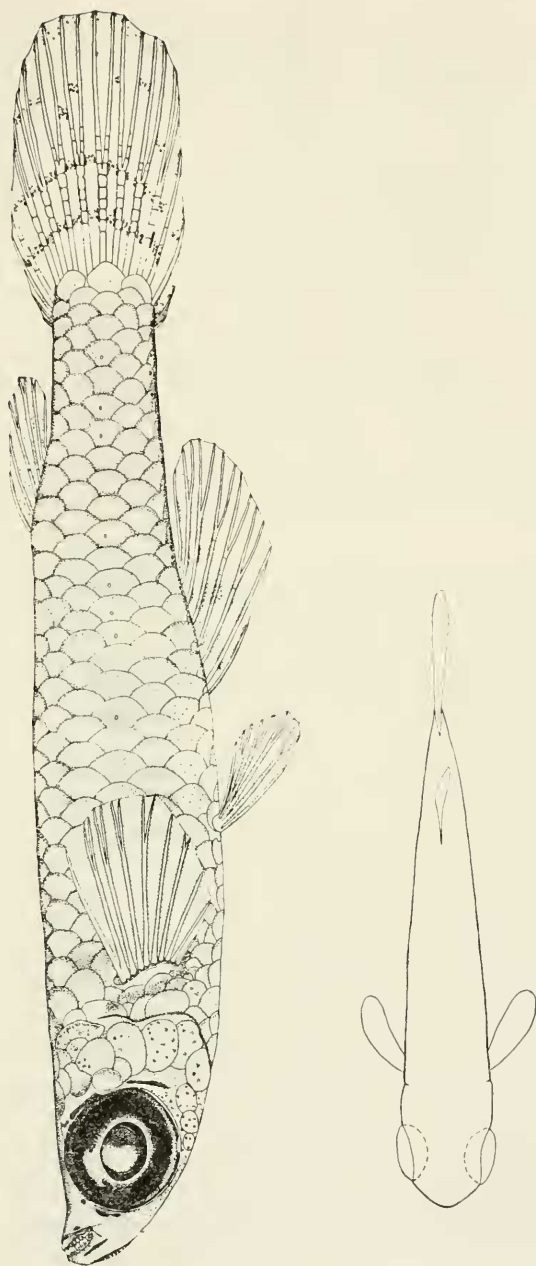


Fig. 1. *Fluviphylax pygmaeus* (Myers and Carvalho). Outline of body, scales, and fins based on alizarin preparation of 18.5-mm male specimen from MZUSP 6245; color pattern, cephalic sensory canals and other superficial features based on slightly smaller specimens from same locality. Inset: dorsal outline.

Morphometric data has not been assembled because superficial examination of the specimens reveals no proportional variations of consequence and because accurate measurements of the small specimens are difficult. The proportions given in the following description were obtained by measurements on a few specimens or by stepping off distances with a pair of dividers and are meant to provide a general impression. Counts of fin rays and scales made on many of the specimens reveal little variation; pectoral, dorsal and anal fin counts vary by only a ray or two.

Body proportions. Greatest depth of body 5.0. Least depth of caudal peduncle 9.0. Head 4.0. Eye 2.5 in head. Bony inter-orbital space slightly greater than eye diameter. Snout about .5 eye diameter. Width of mouth about .75 interorbital space. Dorsal fin about same size as pelvic fin, length of dorsal fin base about equal to length of base of first five anal rays. Anal fin far larger than dorsal fin, and slightly larger than pectoral fin. Caudal fin distinctly larger than anal fin. Length of caudal peduncle about equal to anal fin base.

Fin rays. Dorsal fin with five or six rays; anal fin usually with eight rays, sometimes nine; in alizarin specimens first two and last two rays of dorsal and anal fins simple, other rays branched. Pectoral fin with 10 or 11 rays, pelvic fin with six rays, caudal fin usually with 17 rays (counts on alizarin preparations reveal eight principal, five upper and four lower procurent caudal fin rays). Rays in all fins without unusual specializations.

Squamation. Scales uniformly cycloid, 25 or 26 in midlateral series. Anteriorly three, slightly posterior to anal origin two, and on caudal peduncle one, rows of scales between midlateral and dorsomedian scale rows. About 18 or 19 scales in median predorsal series from occiput to origin of dorsal fin. Nine scales around caudal peduncle. Seven scales in diagonal series from in front of dorsal fin origin to middle of anal fin base. About five scales along anal fin base. Fins themselves scaleless except for two rows of normal-sized scales extending beyond hypural fan onto proximal portion of caudal fin. Scales on either side of genital region unenlarged and unspecialized.

I tentatively interpret the squamation on the dorsum of the head in *Fluviphylax* (Fig. 2) as typically consisting of a single *h* scale, a single *g* scale (which overlaps the *e* scales in some specimens but not in others), two *e* scales, two *d* scales, and a single *a* scale. Perhaps owing to the exceptionally large eyes, the *a* scale appears to be further forward than usual. Some specimens appear to have two

scales in the "a" position. Some specimens have a small scale anterior to the *h* scale. There are a pair of scales on either side of the head over the supraorbital portion of the frontal bone. This is a simplified pattern similar to that probably found in many unrelated

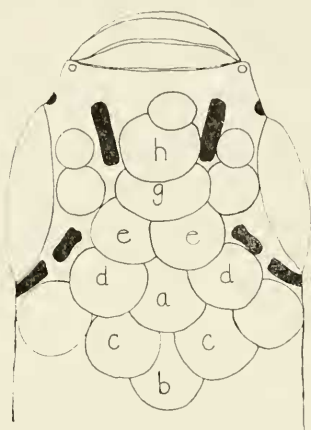


Fig. 2. Scale pattern on dorsum of head in 15.1-mm specimen.

forms in which the pattern has been secondarily reduced, including *Epiplatys sexfasciatus*, young *Nothobranchius* (or *Aphyosemion*?) *sjoestedti*, and perhaps young *Pantanodon podoxys* (Whitehead, 1962, figs. 12 and 13).

Coloration. The MZUSP lots (including several not listed above) I have examined vary from those in which the specimens are relatively dark and have markings that stand out to others in which the specimens are quite pale and the markings are washed out. I am fairly confident, however, that all represent the same species. The coloration is sexually dimorphic. In females in all lots there is a more or less sharp demarcation between the relatively dark sides and the light belly, while the fins are clear or slightly dusky, but never have distinct markings. In males, on the other hand, the body is more uniformly colored, the belly about the same color as the sides; the sides usually bear a series of hazy, lozenge-shaped, vertical bars, from two or three restricted to the pectoral region to a dozen or so for the length of the body; the dorsal, anal and caudal fins bear concentrations of melanophores (see Fig. 1).

Scant observations were made on coloration in live *Fluviphylax* during the EPA fieldwork in which I participated, since all were

taken during rotenone collecting and were seen but briefly before they had to be preserved. I distinctly recall that they lack the shimmering bluish-greenish reflections on the sides possessed by African Procatopodinae such as *Poropanchax rancureli* and *Aplocheilichthys shiotzi*. The most striking feature of their coloration is a silvery sheen, presumably guanine, on the entire dorsal surface of the eyes. As a little *Fluviphylax* swims along just below the water's surface, two brilliant silvery dots (surprisingly large considering the size of the fish) are seen moving along.

Sex ratios. In some MZUSP lots almost all intermediate-sized specimens bear eggs, the smallest specimens are quite evidently immature, and only a few of the largest individuals are males. This suggests they might be protogynous hermaphrodites. In other lots, however, nearly half of the specimens, including ones as small as 12.5-14 mm, are males.

ECOLOGY

Fluviphylax has been collected along large stretches of the Lower and Middle Amazon, and presumably occurs in suitable habitats throughout the Amazon basin. I remember catching a single specimen near the mouth of the Rio Jauaperi, well up on the Rio Negro, but the specimen was lost before it could be preserved. *Fluviphylax* lives in still, shaded, black- or brown-tinted, shallow backwaters, not in the main rivers or even in small, flowing streams. Most fishes in such places are small species. The principal predaceous kinds are likely to be a pair of "dwarf" species of *Acestrorhynchus*, *A. nasutus*, and *A. minimus*, and occasionally *Hoplias*, *Hoplerythrinus*, or *Potamorhaphis*. In EPA collections *Fluviphylax* also is associated with *Crenuchus*, *Curimatopsis*, several species of *Hemigrammus* and *Hyphessobrycon*, *Iguanodectes*, *Hypopomus*, a minute species of *Trichomycterus*, two or three species of *Apistogramma*, *Cichlasoma festivum*, two tiny species of *Microphilypnus*, *Poecilia* (*Pamphorichthys*) *minor*, and other small species. *Rivulus* also occurs together with *Fluviphylax*, but my impression is that *Fluviphylax* tends to stay in more open water than *Rivulus*, which during the dry season is likely to be left in small pools that are drying up. *Rivulus* frequently occurs singly in water only inches deep and probably spends long periods relatively motionless, whereas *Fluviphylax* is usually over deeper water and possibly maintains small schools near the surface. Stomach contents of numerous specimens contain minute insect larvae or adults (no other food items observed).

Fluviophylax is evidently the smallest known oviparous cyprinodont. In all sizable samples obtained by EPA (representing the months of February-April and September-October) small specimens predominate, despite probable sampling errors favoring larger specimens. This indicates that reproduction occurs throughout much of the year, perhaps year-round. If so, the bulk of the population probably is sexually immature at all times, and I would not be surprised if the average size of an individual in these populations falls between 9 and 11 mm. If we can judge from other small oviparous cyprinodonts, hatchlings are probably between 4 and 6 mm.

OSTEOLOGY

Figures 3-13 (Reduced to same scale.)

This account of the osteology of *Fluviophylax* is based on four specimens (11.5, 14.4, 16.5 and 17.0 mm) from the MZUSP 5590 and two specimens (17.8 and 18.5 mm) from MZUSP 6245. The figures are based on the larger two of the four specimens from MZUSP 5590. All statements which follow were based on observations verified in at least two or three specimens. The 11.5 mm specimen is well ossified; differences noted between it and larger specimens are 1) failure of nasal bones to ossify; 2) less development of anterolateral parasphenoid wings; and 3) presence of a sixth branchiostegal ray on left side. No osteological differences attributable to secondary sexual dimorphism were detected.

Braincase (Figs. 3-5). Braincase typically cyprinodontoid in appearance (cf. numerous figures of cyprinodont crania in dorsal view in Rosen and Bailey, 1963). Cranium very slightly tapered anteriorly. Supraorbital processes of frontal well developed; frontals with a concavity behind supraorbital process for reception of dermosphenotic, which lies over sphenotic and snugly against frontal. Mesethmoid a thin ossification folded back on itself at its anterior margin to form a double lamina open posteriorly. Mesethmoid not contacting prefrontals. Preopercle, parietals, and basisphenoid bones absent. Anterolateral parasphenoid wings moderately developed, not contacting pterosphenoids to form posterior myodomes (in cyprinodonts anterolateral parasphenoid processes play the role corresponding to that of the basisphenoid in other fish groups). Dorsal border of foramen magnum formed exclusively by exoccipital bones. Supraoccipital bone typically cyprinodontoid in form. Exoccipitals and epiotics without posteriorly-directed processes or wings. Supraoccipital with a close-set pair of short

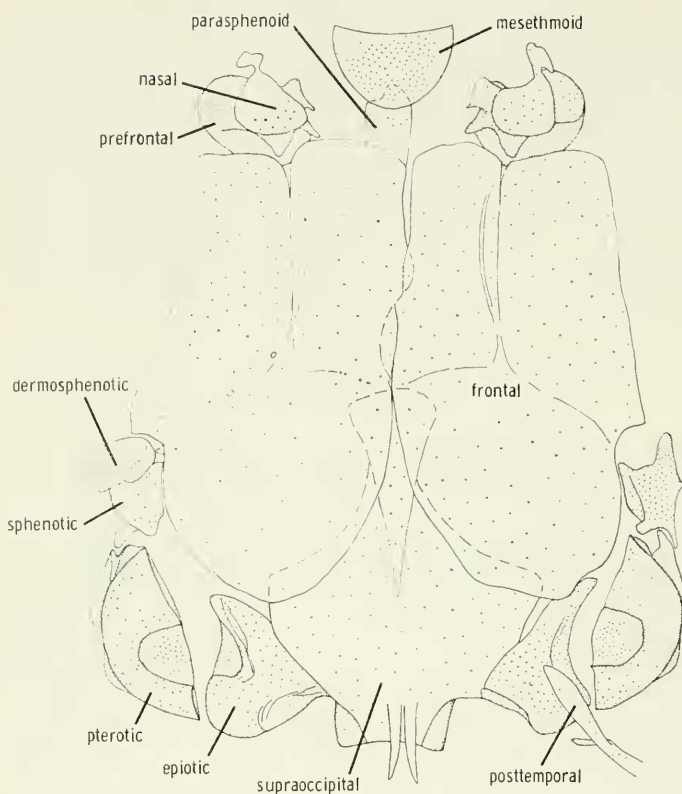


Fig. 3. Dorsal view of cranium, 16.5-mm specimen (all osteological figures based on specimens from MZUSP 5590).

spines extending straight back near dorsal midline. Basicranium with a basioccipital and two exoccipital condyles (Fig. 5). Ventral surfaces of pterotic and sphenotic bones with well-developed sockets for articulation of hyomandibular bone (Fig. 4).

Facial bones (Figs. 6, 7). Nasal bone small and weakly ossified. Lacrimal bone weakly ossified, its shape seemingly determined solely by its function as a bony trough for preorbital segment of cephalic sensory canal system and its relation to anterior margin of eye. Bony trough in upper arm of preopercle for postorbital segment of cephalic canal system extremely close to hind border of eye. Bony troughs for segments of cephalic canal system formed

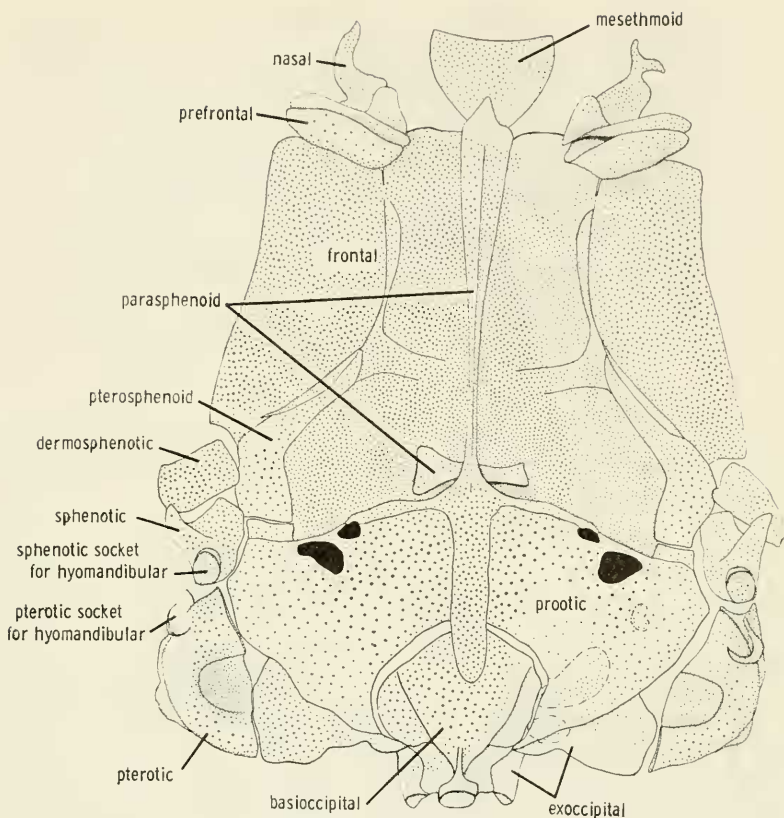


Fig. 4. Ventral view of cranium, 16.5-mm specimen.

only by lacrimal, preopercle and dermosphenotic bones. The very large eye is apparently unassociated with any radical modifications or displacements of bones. Subopercle very large, forming entire posterior margin of gill cover. Upper arm of subopercle terminating in a weak flange forming dorsal margin of an externally visible concavity in opercular margin just below dorsal origin of gill slit. Lower arm of subopercle with a strong, dorsally-directed flange lying between opercle and interopercle. Interopercle very elongate.

Jaws and jaw suspension (Figs. 6, 7). The jaws do not differ from what one would expect in a small, surface- or near-surface-feeding, insectivorous cyprinodont. Premaxillaries moderately pro-

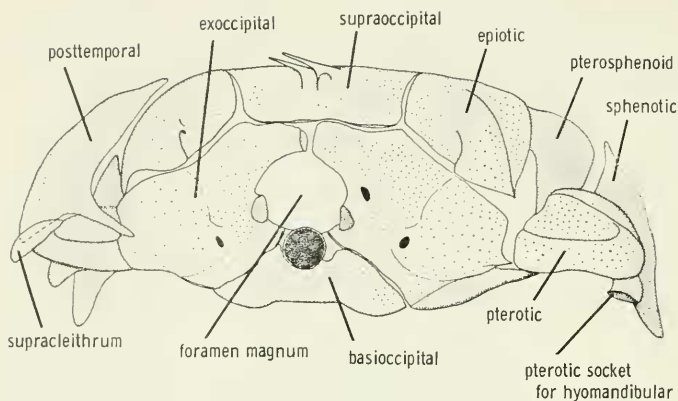


Fig. 5. Occipital view of cranium, 17.0-mm specimen. Pterosphenoïd visible because frontal and dermosphenotic bones have been removed. Viewed from angle to right of fish.

tractile, ascending premaxillary processes broad-based and short, with rounded posterior margins. Maxillaries slender, with well-developed mesial and palatine processes. Mesial processes ligamentously attached to ventral surface of ascending premaxillary processes; back and forth movement of premaxillaries accompanied by equal movement of mesial maxillary processes, and when transmitted to distal portion of maxillaries (beyond palatine processes) these rotate on their axes while remaining in more or less the same vertical plane. An 11.5-mm specimen has about 26 teeth in upper jaw and 22 in lower; a 16.5-mm specimen, about 35-40 teeth in both jaws.

Hyomandibular bone with well-developed, separate joints for articulation of pterotic and sphenotic bones. Palatine, ectopterygoid, and entopterygoid intimately united (for discussion of these elements in cyprinodonts see Rosen, 1964: 232, fig. 10). Symplectic bone elongate. Quadrate with a slender, posteriorly-directed extension. Metapterygoid absent.

Hyoid and pharyngeal arches (Figs. 8, 9). The hyoid arch has the following peculiarities: 1) hypohyal of each side a single, undivided element; 2) interhyal absent; 3) branchiostegal rays, usually five on each side, articulating with ceratohyal; 4) urohyal with a strong, dorsally-directed process at its anterior end; and 5) epihyal and ceratohyal not rigidly joined by a dorsal bony ridge.

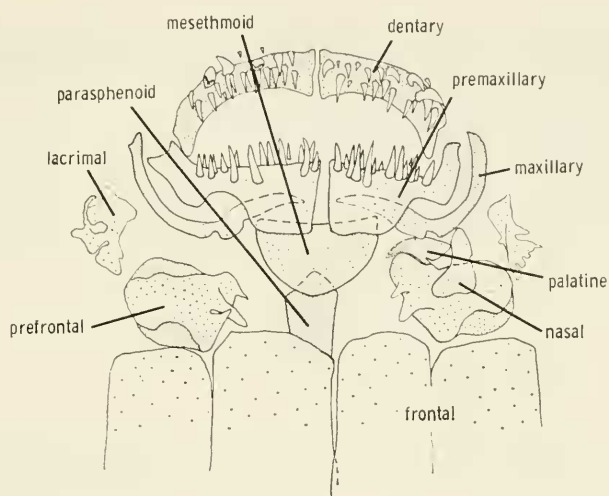


Fig. 6. Dorsal view of jaws and anterior bones of head, 16.5-mm specimen; head tilted back.

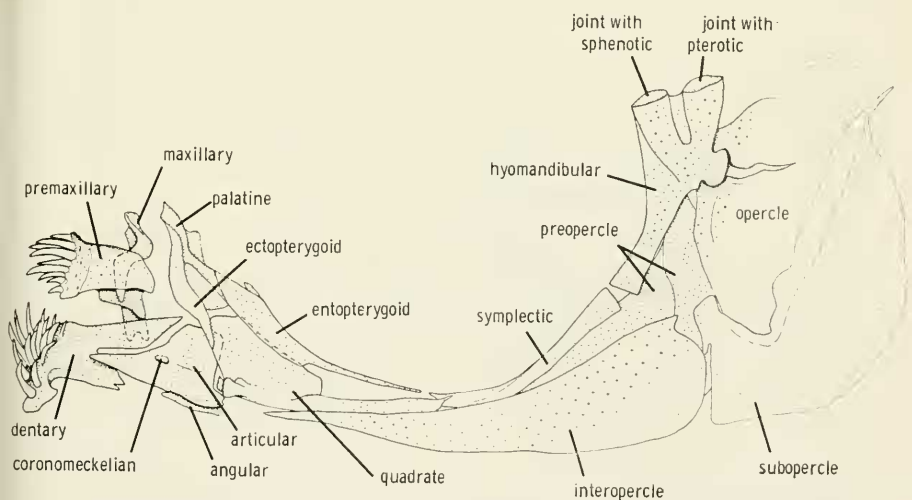


Fig. 7. Internal view of jaws, jaw suspension and opercular elements, 16.5-mm specimen.

Branchiostegal rays usually simple, but in 17.8-mm specimen anteriormost ray on one side with a hooklike, medially-directed process midway on its length.

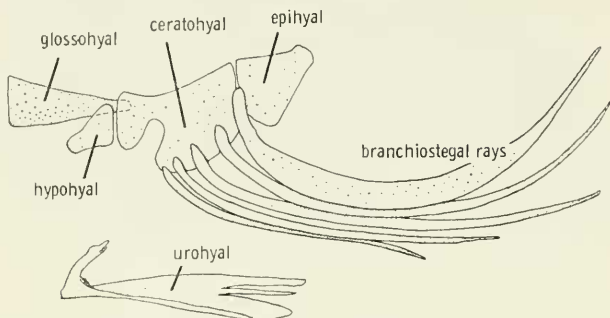


Fig. 8. External view of hyoid arch and urohyal (separated), 16.5-mm specimen.

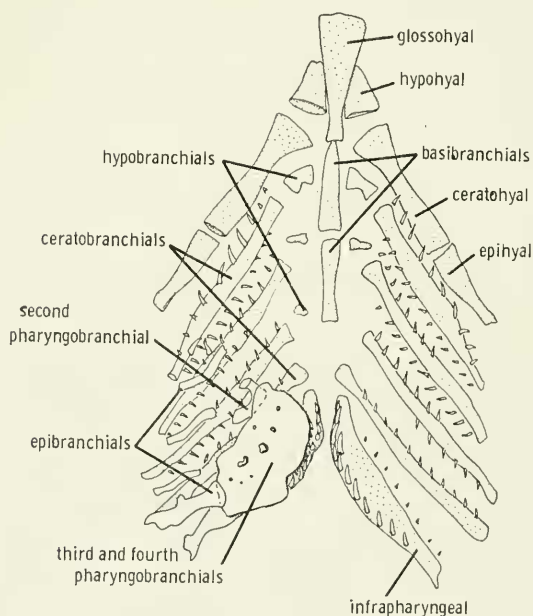


Fig. 9. Dorsal view of hyoid and pharyngeal arches, with dorsal elements shown on left side only, 16.5-mm specimen. Third hypobranchial on right side not ossified in this specimen; ossified in other specimens.

Pharyngeal arches with two elongate ossified basibranchials. First pharyngobranchial absent. Second pharyngobranchial intimately associated with but separate from upper pharyngeal plate, toothless in some specimens, in others bearing four to six conical teeth. Upper pharyngeals, presumably consisting of united third and fourth pharyngobranchials, with a dense patch of conical teeth. Lower pharyngeals of left and right sides not in contact, with two or three irregular rows of conical teeth.



Fig. 10. Frontal view of first vertebra, 16.5-mm specimen.

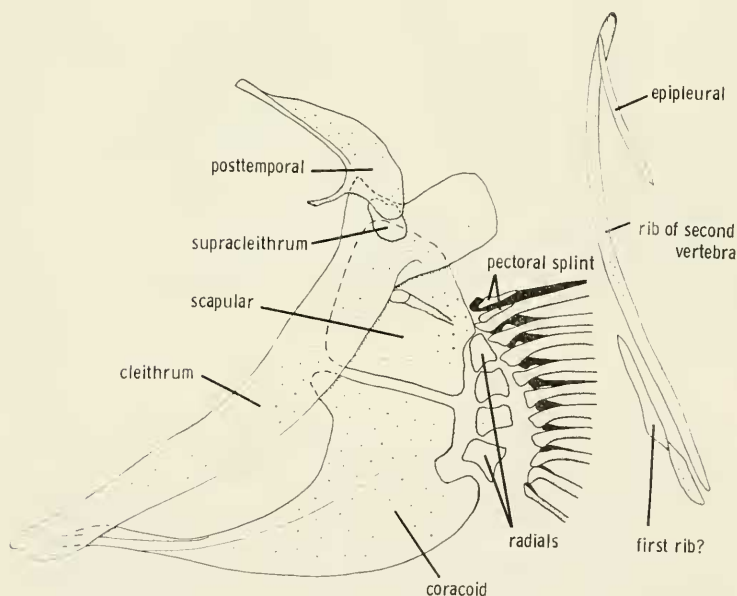


Fig. 11. External view of pectoral girdle, 16.5-mm specimen; first and second ribs drawn separately; in normal position they lie directly behind the radial bones, or behind radial bones and articulations with pectoral rays.

Vertebral column. Vertebrae 26 excluding hypural, 12 abdominal and 14 caudal or 13 abdominal and 13 caudal. First vertebra (Fig. 10) with complete neural arch, three condylar facets, and associated pair of epipleural intermuscular bones, without transverse processes or ribs. A small element associated with the distal end of the rib of the second vertebra is probably the true first rib (Fig. 11). This element is characteristic of cyprinodontoids; in *Oryzias melastigma* it is unusually long. Rosen and Bailey (1963: 31) interpreted what is evidently the same element in Poeciliidae as a secondary postcleithrum. In *Fluviophylax* it lies in the body wall, and is separated from the pectoral girdle by the deep pocket internal to the pectoral fin base. Remaining abdominal vertebrae with large, stout transverse processes to which are attached proximal tip of ribs, and simple epipleurals. In some specimens epipleurals fail to develop in association with posterior abdominal vertebrae. Caudal vertebrae lacking epipleurals. Haemal canals moderately large.

Pectoral girdle (Fig. 11). Posttemporal bone forked, upper limb articulating with epiotic, lower with exoccipital (intercalar absent). Supracleithrum small, scalelike, interposed between posttemporal and cleithrum. Scapular foramen present. Cleithrum rather slender. Lower limb of coracoid slender, its anterior end extending to near anteroventral tip of cleithrum; space between cleithrum and coracoid large. Postcleithra absent. Pectoral radials four. Pectoral splint present, consisting of two very short, bony splints tightly adherent to dorsal surface of ray halves of uppermost pectoral ray.

Pelvic girdle (Fig. 12). Distal tip of fifth rib ligamentously attached to dorsal surface of median pelvic projection. Posteriorly directed bony process of pelvic girdle very short, lacking in some specimens.

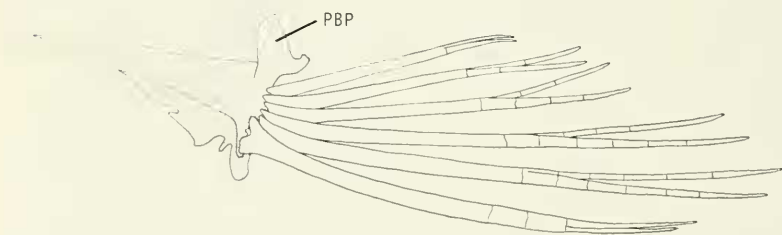


Fig. 12. Ventral view of left pelvic girdle and fin rays, 17.0-mm specimen. PBP = posteriorly directed bony process.

Caudal skeleton (Fig. 13). Hypural fan fused into a solid unit, even in 11.5-mm specimen, to which six of the eight principal caudal rays attach. Epural and haemal spines of hypural centrum each bearing a single principal ray.

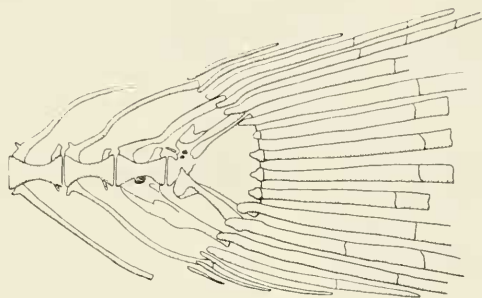


Fig. 13. Last three vertebrae and caudal skeleton, 11.5-mm specimen. Tiny separate element just above hypural centrum not evident in other specimens.

RELATIONSHIPS

The osteological characteristics of *Fluviophylax* are such that it does not fall automatically in any of the groups into which Sethi (1960) divided the oviparous cyprinodonts of the world (it is obviously unrelated to *Pantanodontinae* [Whitehead, 1962; Rosen, 1965] which Sethi did not consider), but they indicate that its relationships either lie with *Procatopodinae* or else with *Fundulinae*, and not with *Rivulinae*. In order to facilitate comparisons these characters of *Fluviophylax* are listed here (the order is similar to that employed by Sethi).

1. Mesethmoid a bony, double lamina.
2. Prevomer absent.
3. Nasal bones reduced.
4. Dermosphenotic prominent.
5. Parietals absent.
6. Anterolateral parasphenoid processes short, not contacting pterosphenooids.
7. Foramen magnum bordered exclusively by exoccipitals and basioccipital.
8. Exoccipital and basioccipital condyles well developed.
9. Transverse processes of first vertebra meeting dorsally, not articulating with occiput.
10. No distinct gap between first and second vertebrae.
11. Transverse processes of precaudal vertebrae stout and elongate.

12. Epiotic processes absent.
13. Metapterygoids absent.
14. Teeth strictly conical, disposed in two irregular rows on both jaws.
15. Premaxillary processes short and broad, extending over mesial maxillary processes.
16. Mesial maxillary processes large and ligamentously attached to ventral surface of ascending premaxillary processes.
17. Outer maxillary processes weakly developed.
18. Hypohyals consisting of a single element on each side.
19. Branchiostegal rays normally five on each side.
20. Third and fourth pharyngobranchials united.
21. Infrapharyngeals separated.
22. Two ossified basibranchials.
23. Posttemporal bone forked.
24. Supracleithrum present.
25. Postcleithra absent.
26. First rib greatly reduced, associated with distal tip of rib of second vertebra.
27. Large space between cleithrum and coracoid.
28. Posteriorly-directed, bony pelvic process short or lacking.
29. Haemal canals moderately large.
30. Hypural fan a solid piece.
31. Vertebrae 26.

Comparison with Rivulinae. Differences between *Fluviphylax* and Rivulinae are numerous and fundamental, the most important being that Rivulinae have a cartilaginous mesethmoid, toothed prevomer, metapterygoid, dorsal and ventral hypohyals on each side, separated third and fourth pharyngobranchials, and a hypural fan divided in two or even (in *Aplocheilus*) three parts. It should be noted that our knowledge of the osteology of *Rivulus* is based on a single species (*R. bondi* Schultz). Although there are many species of *Rivulus*, the genus is very constant in its characters (Myers, 1927: 119) and since Sethi found relatively few differences between *R. bondi* and other genera of Rivulinae it is reasonable to expect only relatively minor differences among various species of *Rivulus*. A number of non-osteological differences between *Rivulus* and *Fluviphylax* were pointed out above in the generic characterization of *Fluviphylax*.

Fluviphylax is a very distinct genus but is notably lacking in bizarre or "unexpected" specializations or distinctive osteological characters that would set it apart readily from all other cyprinodont groups. Most of its osteological characters occur in many or even in most cyprinodont groups, apart from Rivulinae, and thus are of little value in assessing phylogenetic relationships. Regarding character 31, 26 is near the lowest number of vertebrae in cyprinodonts.

Diminutive representatives of any group are likely to have reduced vertebral counts approaching this number. Since an overwhelming proportion of these characters occur in Procatopodinae and Fundulinae, in contrast to other groups, the relationships of *Fluviphylax* may lie with one of these two subfamilies.

Comparison with Procatopodinae. All Procatopodinae in which the osteology has been studied agree with *Fluviphylax* in characters 4-13, 17, 18, 20-22, 24, and 26-30, and one or more species also agree in characters 2, 14, 19, 23 and 25. In *Poropanchax rancureli* the prevomer is absent and the posttemporal is forked about as in *Fluviphylax* (personal observation). Perhaps the most important difference between Procatopodinae and *Fluviphylax* is that Procatopodinae have a cartilaginous mesethmoid and in none of the Procatopodinae is the mouth position quite as in *Fluviphylax*. On the other hand, the elevated pectoral fin position is virtually identical in *Fluviphylax* and Procatopodinae. In *Poropanchax rancureli* the three uppermost pectoral rays articulate with the scapula and the portions of the cleithra that form the posterior wall of the gill chambers are almost vertical, whereas in *Fluviphylax* only the uppermost pectoral ray articulates with the scapula and the posterior wall of the gill chambers is oblique. These observations suggest that the elevation of the pectorals in *Fluviphylax* and Procatopodinae may have been achieved in different ways. It should be noted that the pectoral fins are extremely elevated in the remarkable, tiny cyprinodontoid *Horaichthys*, presumably related to *Oryzias* (see Kulkarni, 1940: 379-423, and especially figs. 2 and 18). In *Horaichthys*, incidentally, the dorsal fin is very small and its position is more posterior than in any other cyprinodontoid. This suggests that the high-set pectorals, small, posteriorly-placed dorsals and reduced body size in many procatopodins and in *Fluviphylax* are functionally correlated characters.

Comparison with Fundulinae. All Fundulinae in which the osteology has been worked out agree with *Fluviphylax* in characters 1, 4, 7-11, 13, 15, 16, 18, 20-24, 26 and 28-30, and one or more species also agree in characters 6, 12, 14, 17, 19 and 25. The most important differences between Fundulinae and *Fluviphylax* appear to be that Fundulinae have a prevomer and parietals, and low-set pectoral fins with a restricted space between coracoid and cleithrum. Pectoral fin position and amount of space between coracoid and cleithrum may well be functionally correlated characters. The prevomer and probably the parietals have been lost in several cyprinodont lines, so their absence is not wholly unexpected in a

form so tiny as *Fluviphylax*. Most adult Fundulinae have posteriorly-directed epiotic processes but these develop late and are sometimes unformed in specimens the size of *Fluviphylax*. Of described Fundulinae, perhaps *Fundulus notatus* bears the greatest superficial resemblance to *Fluviphylax*. A fish derived from *F. notatus* but smaller (and with fewer vertebrae), with enlarged eyes, open instead of tubular cephalic laterosensory canals, a considerably shortened snout (involving loss of prevomer, reduction of nasal and lacrimal bones, and shortening of ascending premaxillary processes), slightly elevated pectoral fins (with an enlarged space between coracoid and cleithrum), and a more posteriorly placed dorsal fin (with fewer rays) would be exceedingly like *Fluviphylax*.

Whatever its relationships may be, *Fluviphylax* does not belong in any of the recognized subfamilies. Therefore a new subfamily is proposed for it.

FLUVIPHYLACINAE new subfamily

A subfamily of very small, oviparous cyprinodonts with exceptionally large eyes, free orbital rim, dorsal fin placed far posteriorly, pectoral fin set high, tips of pectoral fin rays extending beyond base of pelvic fins. The main osteological characters of the subfamily are listed and discussed above. The subfamily, perhaps ecologically equivalent to some of the African Procatopodinae, is known only from the Amazon basin.

DISCUSSION

Fluviphylax is closest phenetically to Procatopodinae, and perhaps it is also closest to them phyletically, but relationship with Fundulinae is too strong a possibility to be ignored. At least until the phyletic relationships of *Fluviphylax* are clearer it is best to recognize it as forming a monotypic subfamily, the Fluviphylacinae. In considering the relationships of *Fluviphylax*, I have refrained on purpose from zoogeographic speculation. In this instance zoogeographic aspects are so controversial they can only serve to confuse matters until relationships are clearly understood. That Procatopodinae are almost exclusively restricted to continental Africa is insufficient grounds to disqualify them as possible relatives of *Fluviphylax*. In this connection, I have tended to think of *Fluviphylax* as relatively recently derived simply because of its tiny size, a conclusion which may be quite erroneous.

Fluviphylax illustrates a feature of cyprinodont distribution that should be elaborated, namely that the tiniest forms occur in the midst of the world's richest fresh water fish fauna (Amazonas), whereas the relatively giant forms are found in situations geographically or ecologically isolated from rich fish faunas. The only other described oviparous cyprinodont (if it is truly an oviparous cyprinodont, and adult) as small as *Fluviphylax* is *Hubbsichthys laurae* Schultz, represented by a single 14-mm specimen from "Pampán, Estado de Trujillo, Venezuela, probably Río Motatán drainage" (Schultz, 1949: 96-97). The smallest viviparous cyprinodont, *Poecilia (Pamphorichthys) minor* (Garman), is Amazonian. As stated by Garman (1895: 92), "the length of the males is about seven-tenths of an inch and that of the females about eight" and "females of three-fourths of an inch in total length contain fully developed embryos." I have examined a 14.5-mm specimen collected by EPA in Lago Parauacui, near Oriximina, state of Pará, in which the gonopodium is fully mature and serrae are formed on the second ray in the pelvic fins of both sides (*cf.* Hubbs and Hubbs, 1945: 295-296, fig. 2). The types were obtained by the Thayer Expedition near Villa Bella, roughly a hundred miles up the main Amazon River from Obidos and about the same distance from Oriximina (for a map showing the route of the Thayer Expedition, as well as the routes of Spix and Martius, Castelnau, Natterer and Schomburgk, see Eigenmann, 1917, pl. 1).

Myers (1966: 769-771) pointed out that poeciliids apparently radiated into forms of diverse ecology and size in "the Ostariophysan vacuum" of Central America before Cichlidae arrived there. The advent of cichlids may have cut down this diversity, especially in the larger, stream-inhabiting poeciliids, "leaving the many smaller poeciliids, as in North and South America, only in what might be termed peripheral habitats." *Pamphorichthys* provides a beautiful example of a tiny poeciliid in a cichlid- and characid-rich environment.

Regarding the largest cyprinodonts, the Orestiidae occur only in Andean lakes and associated rivers and streams in Bolivia, Peru, and northern Chile at altitudes between eight and 16 thousand feet (Eigenmann and Allen, 1942). *Anableps*, *Belonesox*, and the largest species of *Fundulus* and of *Poecilia* all are brackish-water forms generally restricted to estuarine or near-estuarine habitats or are euryhaline and tend to occur either in fresh water where the fresh water fish fauna is relatively poor (e.g., *Belonesox*) or else in marine and semi-marine habitats where the marine fish fauna is

relatively poor (e.g., most of the largest species of *Fundulus*). I suspect that *Belonesox* would be unable to coexist with the predatory characoids *Hoplias* or *Ctenolucius*, and that this may have helped shape the southern boundaries of its range. Orestiidae may be unable to withstand the introduction of gamefish such as trout into their mountain retreats.

During fieldwork in Ghana I gained the impression that the largest Rivulinae there, particularly *Epiplatys*, usually occur in isolated situations such as in small streams above waterfalls or along the margins of swampy areas, where they are sometimes the only fishes present. I suspect that the largest Amazonian Rivulinae tend to be similarly isolated. The largest West African procatopodin, *Aplocheilichthys spilauचना*, generally is restricted to estuarine or near-estuarine habitats and the lowermost reaches of rivers. In a recent account of the Procatopodinae of Ghana, Scheel (1968: 277) did not mention the presence of this species there. It is abundant near the mouths of the Volta and Tano rivers and probably occurs in suitable habitats along the entire coast of Ghana. It is the only member of the Procatopodinae to occur on both sides of the Dahomey Gap, a fact explained by its essentially estuarine distribution. The species has been recorded from Senegal to lower Congo (Boulenger, 1915: 62), and from the island of Fernando Póo (Scheel, 1968: 278). It is apparently the only procatopodin to have reached a locality separated by the sea from continental Africa. It may have reached there in the not-too-distant past when the island probably was connected to the mainland, some sixty miles distant. The Procatopodinae, incidentally, may qualify as primary freshwater fishes, but we need more physio-ecological data to determine this.

Hoedeman (1956-61) worked out supposed homologies between scales in the dorsocephalic squamation in a large number of cyprinodont species and used this information as a basis for suggesting relationships at various taxonomic levels. Species and species-groups do have characteristic scale patterns, and these may be useful in determining relationships between forms in which the patterns have remained relatively unchanged. But the difficulties of interpretation increase proportionately as the number of scales changes or the patterns are radically different. The fundamental problem involves homologies. In two of the three major criteria for determining whether structures are homologous, morphology and embryology, the head scales presumably are all identical. That is, they have the same histological structure, and so far as we

know, arise from anlage which are indistinguishable one from another.

Hoedeman frequently explained reductions in number of head scales as being due to "fusions." Surely decreases and increases in the number of head scales correspond to the formation of fewer or more scale anlage, not to fusion or the analogous process implied, "splitting" of scales. Change in scale number probably is accompanied by partial or total rearrangement of spacing between scale anlage in an otherwise essentially uniform field with scale-forming potential. If this is so, is it not erroneous to apply homologies as Hoedeman has done?

The sole criterion Hoedeman used to determine homologies is that of relationships to other structures. He assumed that the scale overlying the pineal organ is homologous in all cyprinodonts (Hoedeman, 1958a: 23). He did not point out any anatomical connection between the pineal gland and this scale, however, and the relationship would seem to depend entirely on the superficial characteristic of position. Using this scale, the "*a scale*," for a starting point, Hoedeman extrapolated the rest of his homologies according to the spatial relationships of the remaining scales to it and to each other. This is clearly a precarious operation. Granted that all cyprinodonts develop dorsocephalic squamation, one would expect to find a scale more or less directly over the pineal organ in every species. In fact, the exact position of the scale over the pineal organ varies considerably, and sometimes there are two scales side by side more or less directly above it. In Rivulinae, the scale in the "*a*" position usually is overlapped by all of the scales neighboring it, whereas in various species belonging to other sub-families it is the topmost scale (Hoedeman, 1958a)!

On the other hand, some of the relationships between scales pointed out by Hoedeman are remarkably constant; furthermore, within groups the scales tend to remain in the same relationship to segments of the cephalic sensory canal system. In many cyprinodonts (*cf.* Rosen and Mendelson, 1960; Whitehead, 1962, fig. 12) what I would interpret as the "*g scale*" is unpaired and has a segment of the supraorbital cephalic sensory canal on either side of it; occasionally it is the anteriormost scale. Immediately behind it is a pair of "*e scales*," which are frequently notched at their posterolateral borders where they are approached by the dorsal-most portion of the posterior infraorbital canal. Behind these *e scales* is a median scale (sometimes paired), the *a scale*, near the posterior margin of the eye. In cyprinodonts with such a pattern

perhaps we may speak in terms of homologies between scales in corresponding positions in different species.

As I have pointed out in another connection (Roberts, 1967: 251-252) reduction or loss of structures, which is to be expected in small species, frequently leads to convergent characters. In *Pantanodon podoxys* (Whitehead, 1962: 125-126, fig. 13), as in *Fluviphylax*, the dorsocephalic squamation is so reduced that it is of no help in assessing relationships. In the interpretation Whitehead hesitantly decided upon, *Pantanodon* has a large *h* scale, two *g* scales, two *e* scales, and a single *a* scale. According to this arrangement, not only is there a pair of *g* scales, but the *a* scale is further posterior than in any other cyprinodont! If homologies can be drawn between the scales in *Pantanodon* and other cyprinodonts, one might re-interpret Whitehead's two *e* scales as a pair of *a* scales, his pair of *g* scales as *e* scales (which are usually paired), and his *h* scale as a *g* scale (which is usually single). When this is done, it turns out that the dorsocephalic squamation in young *Pantanodon podoxys* is rather similar to that in *Fluviphylax*.

The remarkable silvery sheen on the dorsum of the eyes of *Fluviphylax* deserves further comment. A silvery sheen on the dorsal surface of the eyes is characteristic of certain African lamp-eyes (Procatopodinae) and also, surprisingly, of *Oryzias melastigma*; a similar color feature occurs in the little atherinoid *Pseudomugil signatus*, also known as the Australian Blue-eye (personal communication from N. R. Foster). An analogous silvery color, brilliantly visible when the fishes are viewed from above as they swim near the surface, is the shining occipital spot in *Aplocheilichthys spilarchena*, *Aplocheilus panchax*, *A. lineatus*, some species of *Epiplatys*, *Fundulus olivaceus*, *F. nolti* (the Starhead topminnow), and *F. notatus* (personal communication from N. R. Foster and G. S. Myers). Miehe (1911) suggested that the occipital spot in *Aplocheilus panchax* facilitates capture of the insects it preys upon by luring them closer to the water surface. A more basic function may be to reflect harmful radiations so that they do not pass through the brain or eyes, as the case may be. In *Fluviphylax*, which generally inhabits shaded places, the eyes' silvery mantle may lessen the need for visual accommodation and minimize the dazzling effect of bright light as the fish swims into a sunlit area.

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